THE COINCIDENT DISTRIBUTION OF RELATED SPECIES OF PELAGIC ORGANISMS AS ILLUSTRATED BY THE CHÆTOGNATHA.

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No small part of the diversification of the organic world has taken place in the open sea. Whether we accept the view that the littoral and abyssal faunas are derivatives of the pelagic, or regard the latter as secondarily derived along many lines from the organisms of the shore and bottom, the fact remains that many groups have undergone great diversification both in the specific and in higher categories in the pelagic habitat. Illustrations of this process are to be found in the diatoms, the Protozoa (notably the Foraminifera, Radiolaria, Dinoflagellata and Tintinnoina), in the Scyphomedusæ, Siphonophora, and Ctenophora, Ostracoda, Schizopoda, Amphipoda, Decapoda, Heteropoda, Pteropoda, Cephalopoda, and Tunicata and certain families of fishes. The Nemertini, Annelida, Rotifera, Holothuroidea and the Hemiptera are sparingly represented. One class, the Chætognatha, are exclusively marine and pelagic, and their affinities are with the more primitive types of invertebrates. It seems probable that their entire evolution, or at least their generic and specific differentiation has taken place in the marine habitat. Their present distribution is therefore of prime interest because of its bearing on the relation of isolation to the origin and preservation of species.

Barriers are far less in evidence in the environment of the pelagic fauna than in that of the shore or of the land. A few instances in limited regions along the margins of great ocean currents as, for example, along the edges of the Gulf Stream or in horizontally stratified waters, there are abrupt transitions in temperature, but in the main the changes in temperature, illumination, density, and substances in solution or suspension, are so gradual that zoological provinces are delimited with difficulty and mainly in terms of temperature, on the high seas away from the influence of

shore conditions. In a large and somewhat vague way isotherms and isothermobaths constitute the barriers of the sea. Many, and in some groups, most of the pelagic species are wide-ranging, found in most seas, through a greater or less range of temperature. The pelagic fauna has thus a considerable cosmopolitan element and part of the differences which result in the contrasted poverty and richness of pelagic fauna are due to changes in the *numbers of individuals* and in the proportionate representation of the various components, as much as, or even more, than to *restrictions in the distribution of species*. In so far as the species of any group of related organisms establish themselves throughout a wide, coincident or overlapping range, in like degree isolation becomes problematical as a factor in the origin of new or preservation of old species.

Our knowledge of the horizontal and vertical distribution of pelagic organisms is lamentably incomplete and partial, and no less so of the Chætognatha than of other groups. Fowler (:06) calls attention to the fact that he finds no published record of a single *species* of that group between 160° E and 80° W, nearly the whole of the Pacific Ocean! Unfortunately no report was published on the Chætognatha of the Challenger Expedition and the results of later surveys have not yet appeared. We find, however, an excellent summary of the known distribution in Fowler's (:06) report on the 'Siboga' collections, based largely on his Biscayan investigations, Fowler (:05), and the work of Doncaster (:03) on the Maldive and Laccadive fauna, of Aida ('97) on that of Japanese waters, of Steinhaus ('96) and Strodtmann ('92) on collections from the Atlantic, and of various recorders in the lists of the *Conseil permanent pour l' exploration de la Mer*, from the waters of Northern Europe. The data thus assembled by one whose critical knowledge of the species has enabled him to sift out synonyms and eliminate probable errors, are far from being adequate to give a complete or satisfactory presentation of the distribution of Chætognatha in the seas named. They are, nevertheless, of sufficient fulness to afford a basis for the consideration of the extent to which isolation of species prevails in this typical pelagic group of organisms and to mark out clearly the necessity for additional data on vertical distribution and breeding seasons for a critical and final analysis of the problem.

It is the purpose of the present note to call attention to the important contributions which investigators of pelagic life might make to the discussion of this phase of the problems of evolution especially since monographers of pelagic groups are best qualified to judge of the degrees of affinity between the species of the genus and can determine whether the most closely related ones have a coincident or contiguous distribution. It is exceedingly desirable that future expeditions investigating the life of the high seas be equipped for a fuller analysis of the details of vertical distribution and that data on breeding seasons of pelagic species be included in monographs whenever available.

Genus Krohnia

This genus includes three species, *K. hamata*, *K. subtilis*, and *K. pacifica*. The first are two oceanic species of wide distribution, the last an Indo-Austral species of surface neritic distribution. The horizontal area of distribution of the first two species is largely coincident, *K. hamata* being known to extend to higher latitudes (81° N., 52° S.) than *K. subtilis* (60° N., 29° S.). As might be expected from its temperature relations, *K. hamata* is recorded from lower levels in the tropics than is *K. subtilis*. Data on this point are not very complete as *K. subtilis* is not an abundant species. The closing net catches of the Plankton Expedition indicate a maximum depth of 1500 m. for *K. hamata* and 850 m. for *K. subtilis*. The two occur together between 300 and 500 m. (37° N). The extent to which the vertical distribution of the two species overlaps cannot be determined from the available data. Fowler (:05) shows that the size of the individual of *K. hamata* increases with the depth in the Biscayan region. The young, that is, only small specimens, were taken above 500 fathoms and large ones with occasional small ones below that level. The sexual condition at different levels was not noted. The possibility of overlapping distribution is certainly present but contiguous distribution is by no means excluded.

Krohnia hamata is found in the mesoplankton of the Indo-Austral region, where *K. pacifica* is also found, but in surface waters exclusively. These two species were thus contiguous

rather than coincident in their distribution. There is thus little conclusive evidence of coincident distribution in the few species of *Krohnia*.

GENUS SPADELLA

The case of the two species of Spadella, *S. cephaloptera* and *S. draco* the area of distribution of the latter, which is a wide one, includes that of the former which is a neritic species from the northwestern coasts of Europe and the Mediterranean. They are both surface forms and their distribution is of the coincident type.

GENUS SAGITTA

The genus Sagitta as revised by Fowler (:06) includes twenty-one species. Their general horizontal and vertical distribution is shown in the accompanying table taken from Fowler's (:06)

	Neritic	Oceanic	EPIPLANKTON									MESOPLANKTON						
			Atlantic Ocean					Indo-australian Ocean				Atlantic Ocean					Indo-australian Ocean	
			arctic	sub-arctic	N. temperate	tropical	S. temperate	S. temperate	tropical	temp. N. Pacific Ocean	sub-arctic Southern Ocean	arctic	sub-arctic	N. temperate	tropical	S. temperate	S. temperate	tropical
ARCTICA	+	+	+	+	·	·	·	·	+	+	·	·	·	+	·	·	·	·
BEDOTI	+	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·
BIPUNCTATA	+	+	+	+	+	+	+	+	+	+	·	·	·	+	+	·	·	·
DECIPIENS	·	+	·	·	+	·	·	·	·	·	·	·	·	+	·	·	·	·
ELEGANS	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·
ENFLATA	+	+	·	·	+	+	+	+	+	+	·	·	·	·	·	·	·	·
FEROX	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
FURCATA	+	+	·	·	+	?	·	·	·	?	·	·	·	+	?	·	·	·
HEXAPTERA	+	+	+	+	+	+	+	+	+	+	+	·	·	+	+	·	·	·
MACROCEPHALA	·	+	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	+
MINIMA	+	·	·	·	+	·	·	·	·	+	·	·	·	·	·	·	·	·
NEGLECTA	+	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·
PLANCTONIS	+	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·
PULCHRA	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
REGULARIS	+	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·
ROBUSTA	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
SERRATODENTATA	+	+	·	·	+	+	+	·	+	+	+	·	·	+	·	·	·	·
SIBOGAE	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+
WHARTONI	·	+	·	+	·	·	·	·	·	·	·	·	+	·	·	·	·	+
ZETESIOS	·	+	·	·	+	·	·	·	·	·	·	·	·	+	·	·	·	+
HAMATA	+	+	+	+	+	·	·	·	·	·	+	·	+	+	+	·	·	+
PACIFICA	+	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·
SUBTILIS	+	+	·	·	+	+	+	+	+	·	·	·	·	+	+	·	·	+
CEPHALOPTERA	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·
DRACO	+	+	·	·	+	+	+	·	+	+	+	·	·	·	·	·	·	·

FIG. 1.—Geographic Distribution of Chætognatha, after Fowler (:06).

(Siboga) report. *S. bipunctata* is omitted by him from the Indo-Austral region in his text because of the uncertainty of its identification since it is quite similar to the young of several other species in the list. Of the twenty-one species, eleven, including *S. bipunc-*

tata, occur in the Atlantic, ten in the Indo-Austral, eight in Japanese waters, and two in the subantarctic, in the epiplankton. In the mesoplankton of the Atlantic eight species are found, and three in the Indo-Austral. In the larger geographical regions of the Atlantic we find coincidently in the epiplankton, in the Arctic, three species, in the subarctic five, in the north temperate, eight, in the tropical, five, in the south temperate, four; in the

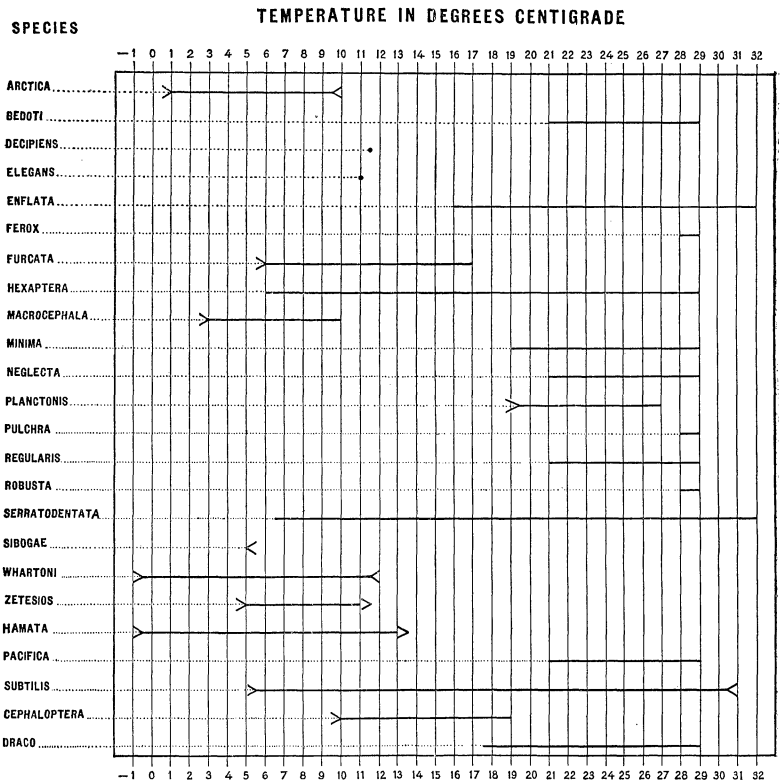

FIG. 2.— Distribution of Chætognatha with reference to temperature.

mesoplankton, two, eight and two species respectively in the subarctic, north temperate and tropical regions. In the Indo-Austral there are three species in the south temperate and ten in the tropical, with three in the mesoplankton of the latter.

The distribution of the species with reference to the temperatures at which they have been recorded is shown in the accompanying table from Fowler's (:06) report.

In the case of Sagitta the distribution is as follows:—

−1°	to	4°	— 3 species
5°	to	10°	— 7
11°	to	15°	— 6
16°	to	20°	— 6
21°	to	25°	— 8
26°	to	32°	— 11

This, in conjunction with the fact that some of the low temperature species belong to the mesoplankton of the tropics, indicates that the center of radiation of the genus has been in the tropics, or that specific differentiation has been relatively more rapid in that region than at the lower temperatures toward the poles.

These broader outlines of the distribution of the species of Sagitta are suggestive of a considerable degree of coincidence of distribution of species, it may be of closely related ones, and prompts to a closer analysis of their relationships and distribution.

The determination of degrees of relationship among species of a genus is a matter of inference from structural details for whose relative values we have no absolute standard. One's judgment is guided by the selection of characters on which classification is based, by experience in dealing with the specific analysis of the material, and subjectively, by the conception of species which one entertains. It is obvious that species differentiated by the slow accumulation of minute fluctuating variations would offer in their modified structures, some clue to the distance of their removal from the parent stock, or from each other. On the other hand the elementary species arising by mutation from *Œnothera lamarckiana* may be regarded as genetically equally related to each other or to the parent stock, but if we base our judgment of the degrees of the relationship which they exhibit solely on the structural characters which distinguish them, we would be forced to conclude that there was considerable disparity of relationship among them. The mutation theory admits a wider latitude in estimating the relationship of species than does the unmodified Darwinian point of view.

We have, however, in Sagitta only the result, and not the process of specific differentiation with which to deal, and are therefore

forced to depend solely upon structural resemblances for the determination of specific relationships.

The species of Sagitta are distinguished, among other less quantitatively expressed characters, by (1) size, (2) ratio of tail to total length, (3) number of jaws, (4) number of anterior and (5) posterior teeth. An analysis of Fowler's (:06) specific diagnoses reveals three groups of related species within which couplets of most closely related species may be noted.

The first of these, the *serratodentata* group, includes five species: *S. serratodentata,* a eurythermal cosmopolitan species with little tendency to sink to deeper waters in the tropics; *S. bedoti,* a neritic surface species from Indo-Austral waters; *S. ferox* and *S. robusta,* neritic and surface species from the Malay and Maldive Archipelagos; and *S. sibogæ,* taken only in hauls from deep water in the Malay Archipelago.

The following table of quantitative characters of the species taken from Fowler's records serves rather to indicate their close resemblance than to differentiate them. Other characters such as proportions, form of the eyes and teeth, assist in diagnosis.

Serratodentata Group.

Species	Length in mm	Tail in % of total length	Jaws	Anterior teeth	Posterior teeth
serratodentata	5–14	28–36	5–7	8–9	16–22
bedoti	13–20	21–28	6–7	8–10	17–29
sibogæ	9–20	21–33	5–7	7–10	16–22
ferox	10–20	29–36	5–6	6–10	9–14
robusta	10–14	25–33	5–7	6–9	10–15

The quantitative characters of the table in conjunction with others not included, suggest that the wide ranging *S. serratodentata* may be the ancestral stock of the couplets *bedoti – sibogæ* and *ferox – robusta,* or more nearly related to that stock than the couplets named.

The 'Siboga' lists indicate that these five species occur in the waters of the Malay Archipelago, but *S. sibogæ* only in collections from the deeper waters. The other four, however, are found together repeatedly in collections from the surface. In the 65 collections in which *Sagitta* occurs all four species appear in 27, three of them in 27, two in 9, and one in but 2, the average percent-

age of coincidence 80%. Of the 65 collections 55 were made at the surface. Four of the five species thus have a coincident distribution, including the mostly closely related couplet *ferox-robusta* and the very closely related *S. bedoti* and *S. serratodentata*. The *bedoti-sibogæ* couplet appear to have a contiguous distribution in the upper and lower levels, respectively, in this region.

A second group of species which show considerable resemblances to each other are *S. hexaptera*, an oceanic, stenohyaline, eurybathic, and eurythermal form; *S. enflata*, a warm water form of wide distribution in the epiplankton of warm-temperate and tropical seas; and *S. pulchra*, a neritic surface form from the Malay and Maldive Archipelagos.

The accompanying table indicates the relationships of the three species of the *hexaptera* group as suggested by the quantitative characters.

Hexaptera Group.

Species	Length in μ	Tail in % of total length	Jaws	Anterior teeth	Posterior teeth
hexaptera	15–70	20–25	6–8	3–4	2–7
pulchra	9–22	18–27	5–7	6–9	10–15
euflata	22–26	16–22	7–9	7–10	12–17

An examination of the 'Siboga' lists shows that the three species occur together in 24 catches, two in 26, and but a single one in 26, the percentage of coincident occurrence being 66%. The most closely related couplet in this group is *pulchra-enflata*, the former a neritic, the latter an oceanic species. These two occur together in the Maldives and also in the 'Siboga' collections, where *S. enflata* is one of the most abundant species. It is found in every one of the 34 collections in which *S. pulchra* appears. Of the 34 coincident occurrences 29 are in surface collections. These three related species have here a coincident distribution and *S. hexaptera* and *S. enflata* have a common distribution over a much wider area.

A third group of related species includes *S. bipunctata*, and two couplets of most closely related species, *furcata–planctonis* and *neglecta–regularis*. Published records indicate that the first named species is a cosmopolitan one of wide range. Difficulties attend its specific determination so that Fowler is of the opinion that it is possibly only an Atlantic neritic form not occurring in Indo-Pacific waters.

The members of the first couplet, *furcata – planctonis*, are Atlantic species, the former of wide distribution, 51° N. to 7° S., in the epiplankton of colder waters (17°) and the mesoplankton of the tropics. The latter occurs only in the epiplankton of the tropics. This couplet of most closely related species has a contiguous rather than a coincident distribution. The distribution of both, however, is overlapped by that of the very closely related *S. bipunctata*. The degrees of relationship as suggested by quantitative characters may be inferred from the accompanying table.

Bipunctata group.

Species	Length	Tail in % of total length	Jaws	Anterior teeth	Posterior teeth.
bipunctata	12–20	21–25	8–10	4–7	8–18
furcata	21–27	22–24	6–7	4–6	9–10
planctonis	17–23	23–26	7–9	6–8	9–10
neglecta	5–10	26–40	5–8	4–6	9–12
regularis	4.5–7	28–40	5–7	2–4	4–6

The members of the second couplet of most closely related species, *S. regularis* and *S. neglecta*, are both surface neritic forms of the Malay Archipelago and Japanese waters. *S. regularis* is neritic also about the Maldives and it may be that Doncaster (:03) overlooked the very similar *S. neglecta* in the collections from these waters. The distribution of these two most closely related species is thus widely overlapping, if not indeed coincident.

The distribution of pelagic organisms, as illustrated by the Chætognatha thus affords several probable instances of the isolation of the members of couplets of most closely related species by isotherms or isothermobaths. This isolation is similar in many of its aspects to that so often found between terrestrial species. It may well be that isolation has been an essential factor in the differentiation of the members of these couplets. Even more general, however, in the pelagic world and among the species of this same group is the phenomenon of the coincident occurrence of couplets, and of larger groups, of most closely related species. We have now no evidence of differential seasons, temperatures, or levels at which breeding might occur in these closely related species. Should these differentials ultimately prove to be absent

we would be forced to conclude that isolation has had no part in the origin, differentiation, and continuance of these related species.

In *Dagitta bipunctata* Miss Stevens (:03) has described a method of close fertilization. As yet we have no light on the extent of its occurrence in other species where the presence of enlarged seminal vesicles and external male parts affords suggestive though not conclusive evidence of external and presumably of cross fertilization. Should all species of Chætognatha prove ultimately to have close fertilization we would have in this a most effective means of isolation.

The apparently wide-spread phenomenon of coincident distribution of related species among pelagic organisms appears to cast some doubt upon the universality of the operation of isolation in the evolution of species as originally maintained by Moritz Wagner ('68) and recently revived by President Jordan (:05).

The contrast here afforded also raises the question whether the two types of 'species' really belong fundamentally to the same category or not. Are those with contiguous distribution, and also many of the geographical species and subspecies of land vertebrates, of a standing exactly equivalent to that of those having a coincident distribution? Are, for example, *S. furcata* and *S. planctonis* merely the extremes of an environmental series beginning in the warm surface waters and ending in deep waters of lower temperature? In other words are they the result, in part at least, of the pressure of the environment? A statistical study of the distribution and variation of such a pelagic couplet and a comparison with a similar study of a couplet having a coincident distribution would be most instructive in indicating whether or not any distinction exists between 'isolation-environmental' species on the one hand and 'selection-mutation (?)' species on the other. Are intermediate forms equally absent in both types of couplets? Is variation similar in kind and in distribution among the individuals of the two types? Above all will the individuals of the isolated couplets maintain their specific integrity if their environments are transposed? And finally will the species with coincident distribution exhibit any greater specific stability under environmental changes than will those produced by the agency of isolation?

Investigators of pelagic organisms have been morphologists so

generally, rather than primarily systematists, that the bearing of the data of the geographical distribution of the organisms with which they have been dealing, upon the broader problems of evolution has been somewhat neglected. It is greatly to be hoped that the life of the sea, primitive, ancient, diversified as it is, may yet shed some light upon the problems which this brief paper can do little more than suggest.

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BIBLIOGRAPHY

AIDA, T.
'97. Chætognaths of Misaki Harbor. Annot. Zool. Jap., Vol. I, pp. 13–21. Tab. III.

DONCASTER, L.
: 03. Chætognatha, with a note on the variation and distribution of the group. Fauna and Geog. of the Maldive and Laccadive Archipelago. Vol. I, pp. 209–218, pl. 13, text figures 39, 40.

FOWLER, G. H.
: 05. Biscayan Plankton collected during a cruise of H. M. S. 'Research,' 1900, Part III.— The Chætognatha. Trans. Linn. Soc. London, Zool. Ser. 2, Vol. X, pp. 55–87, Pls. 4–7.
: 06. The Chætognatha of the Siboga Expedition with a discussion of the synonymy and distribution of the group. Siboga Exped., Monogr. XXI, 85 pp., 3 Pls., 6 Charts.

JORDAN, D. S.
: 05. The origin of species through isolation. Science, N. S. Vol. XXII, pp. 545–562.

STEINHAUS, O.
'96. Die Verbreitung der Chætognathen im sudatlantischen und indischen Ozean. Inaug. Diss., Kiel, 49 pp., 1 Taf., 2 Karten.

STENNS, N. M.
: 03. On the oogenesis and spermatogenesis of Sagitta bipunctata. Zool. Jahrb. Abth. f. Anat., **18,** 227–241, Pl. 20–21.

STRODTMANN,
'92. Die Systematik der Chætognathen. Arch. f. Naturg., Jahrg. LVIII, pp. 333–377, Taf. 17–18.

WAGNER, MORITZ.
'68. Ueber die Darwinsche Theorie in Bezug auf die geographische Verbreitung der Organismen. Sitzber. d. bayer. Akad. d. Wiss. München, Bd. 1, pp. 359–395.